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NET PRIMARY PRODUCTION IN DOUGLAS-FIR ECOSYSTEMS: ITS RELATION TO MOISTURE AND MINERAL NUTRITION

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Efforts to assess productivity of forest sites in the Douglas-fir region have, to date, concentrated on examining relations between site index, age, and yield or on developing empirical associations between soil characteristics and site index. As a result, considerable effort in forest research has gone into developing and improving site index curves (or equations) (King 1966), yield tables or yield functions (McArdle et al. 1961), and soil characteristics and site index relations (Steinbrenner 1979a, 1979b). Even the more sophisticated computer models that are designed to predict forest productivity, such as DFSIM (Curtis et al. 1981), are based on empirical yield functions derived from correlations between volume, age, and site index.

While such models are useful for management purposes, they provide little insight into how various abiotic and biotic site factors interact to influence productivity. Thus a forest manager confronted with a recently established stand or a fresh clearcut cannot predict productivity unless site index is already known. Even then, site index is a measure of past, not future, productivity. Even relations between soil characteristics and site index are of limited utility for a given site. Such relations are developed from past performance of trees on similar sites; these relations may have little bearing on behavior of future managed stands because of potential changes in climatic variables or atmospheric inputs (i.e., acid deposition).

An ideal way of assessing site productivity would be to develop a mechanistic or process-level model combining growth information on the species of concern with information on ecophysiological responses to physical and biological factors. In a sense, this type of model was the objective of much of the ecological modeling conducted by the U.S. International Biological Program. The limited success of such models resulted mainly from their enormous data requirements and the lack of understanding of critical ecosystem and physiological processes.

A more realistic approach to predicting forest productivity would be to use approaches developed in agriculture. These approaches combine observations of plant growth responses to various biotic and abiotic factors of the environment. Informa-

tion on these responses is used in combination with climatic and soil data to predict plant growth.

The objective of this paper is to propose a conceptual model of productivity for Douglas-fir (*Pseudotsuga menziesii*) forests in the Pacific Northwest showing how water and mineral nutrient availability interact to influence stand productivity. The model has shortcomings: (1) it outlines the interactions and thus has no predictive capability; (2) at present it has no way of accounting for the range of management options available to the forest manager. The purpose of this model is simply to demonstrate how potential site productivity is regulated and how abiotic and biotic factors interact to limit actual productivity below the potential productivity for a given site.

FOREST PRODUCTIVITY

In this paper, forest productivity is defined as net primary production (NPP), a term describing total organic matter production by a forest ecosystem. Net primary production is defined as:

$$NPP = GP - Ra$$

where GP is gross photosynthesis and Ra is the sum of plant growth and maintenance respiration. Net primary production is closely analogous to growth as defined by Assmann (1970). An alternative expression of NPP is:

$$NPP = \triangle B + D + G$$

where $\triangle B$ is biomass increment, D is detritus or mortality, and G is grazing. Net primary production can be divided into above- and below-ground components.

There are two main reasons for using net primary production rather than the more traditional forestry-oriented measures of forest growth (such as board foot or cubic volume): (1) Carbon allocation for stem growth is of lower priority than foliage, branch, fine root, and reproductive tissues (Mooney 1972, Waring 1983, Linder and Rook 1984). (2) Foliage and fine roots are the main links between a plant and its external environment. Therefore, the relative amounts of these structures

produced by a forest stand provide valuable information regarding the production potential of a stand.

FACTORS REGULATING FOREST PRODUCTIVITY

Before discussing net primary production and carbon allocation patterns in Douglas-fir stands, it may be useful to discuss the major environmental variables that influence production patterns in the lowland Douglas-fir region. In doing so, it is instructive to compare the role these variables play in the Pacific Northwest relative to other forest ecosystems. Waring and Franklin (1979) rank temperature, moisture, and nutrients in decreasing importance in their effect on the evolution and productivity of Pacific Northwest forests. It is, however, difficult to isolate the influence of these factors because of the numerous and complex interactions occurring between temperature, moisture, and nutrient availability in the field.

Moisture

Forests of the Douglas-fir region occupy a unique environment relative to forests in other parts of North America. In this region, relatively little precipitation occurs during the critical months of the growing season. Table 1 compares two sites in

TABLE 1. Seasonal distribution of precipitation in various regions of the United States.

Location	Total (cm)	% June–August
Montpelier VT	84.6	28.2
Waycross GA	126.0	34.0
Santa Fe NM	35.3	45.0
Hinckley MN	73.7	43.0
Detroit OR	129.9	5.7
Portland OR	107.6	6.5
Medford OR	50.2	7.2
Leavenworth WA	59.0	7.4
Quinault WA	337.1	7.2

Source: United States Weather Bureau.

the Douglas-fir region with representative locations in the major geographic regions of the United States. In all other regions, almost one-third to half of the annual precipitation occurs during June, July, and August, the three prime months of the growing season. In the Pacific Northwest, less than 10% of the annual precipitation occurs during these three months. Moreover, intense summer rainstorms are rare in the Douglas-fir region of the Pacific Northwest; therefore, much of the summer rainfall never reaches the forest floor but is intercepted and evaporates from the canopy back to the atmosphere.

The critical implication of this rainfall distribution pattern is that trees must function through the entire growing season on

water stored in the soil profile or stem sapwood during winter recharge (Waring and Running 1978). In spite of the rainy reputation of the Pacific Northwest, its forests are potentially as prone to drought stress as those in any other forest region of North America. Thus the ability of a soil to retain water for tree growth is a critical factor in determining a site's potential productivity. The water supplying capacity of a given soil is largely a function of its parent material, vegetation, history, and age.

Nutrition

A considerable body of evidence has accumulated showing increased growth by Douglas-fir in response to nitrogen fertilization (Gessel et al. 1969, Miller and Pienaar 1973, Atkinson and Morrison 1975, Harrington and Miller 1979, Gessel et al. 1979). Increased growth has also occasionally been observed in response to additions of other nutrient elements, particularly phosphorus and sulfur (Gessel et al. 1979). Clearly, availability of mineral nutrients plays a role, together with water availability, in regulating productivity of Douglas-fir forests.

Fertilizer response appears to be related to site quality. The magnitude of growth response to fertilizer is greater on sites of low native productivity than on more productive sites. Table 2 shows dry matter production response by Douglas-fir fertilization to urea in several site qualities. These data suggest a pattern in which poorer sites have a greater growth response to nitrogen addition than more productive sites.

Interactions between moisture and nutrition are an important part of a stand's nutrition regime. Moisture availability can be a major factor limiting site fertility through its effects on decomposition, nutrient mineralization, and ion transport rates (Swift et al. 1979, Alexander 1977). For example, Fogel and Cromack (1977) and Edmonds (1979) found decomposition rates to be sensitive to moisture availability in the Pacific

Table 2. Aboveground net primary production changes in response to urea-nitrogen fertilization. Production values are averaged over 200 and 400 kg urea-N/ha treatments.

Site Class**	NPP (Mg/ha·yr)		% Increase
	Control	Urea-N	
I	15.23	17.12	12.4
II	13.93	16.21	16.2*
III	11.42	14.48	26.8*
IV	11.83	14.98	22.8*

*Denotes significant increase at the 95% level.

**Site class is related to dominant Douglas-fir tree height at 50 years: I $>$ 135 ft (41 m); II = 115 to 135 ft (35 to 41 m); III = 95 to 115 ft (29 to 35 m); IV = 75 to 95 ft (23 to 29 m); V = $\leq$ 75 ft (23 m; King 1966).

Northwest. Vitousek et al. (1982) noted somewhat lower nitrogen mineralization and nitrification rates in Douglas-fir stands during dry summers. Similarly, McColl (1969) has shown reduced nutrient availability in Douglas-fir stands during the dry summer months.

Moisture-Nutrition Interactions
In Relation to Productivity

Figure 1 illustrates a proposed conceptual model of how moisture and mineral nutrition interact to influence total site productivity and carbon allocation between above- and belowground components in lowland Douglas-fir forests. In this model, site water balance and nutrient availability appear to play the major roles in regulating net primary production. It might be argued that temperature also plays an important role in regulating productivity—and in fact it does. But the impact of temperature is implicitly included in this model through its effects on the various processes described.

The model shown in Figure 1 is driven by the physical environment a site experiences during the growing season. The critical physical environment is defined in this paper as the balance between soil water storage and evaporative demand during the growing season. The greater the excess of evaporative demand over soil water storage, the drier the site. This site water balance sets an upper limit on the leaf area a site can support as well as the potential productivity that can be achieved.

Leaf surface area is the site where carbon dioxide and light uptake and water loss occur. This critical surface functions as the aboveground interface between a tree and its environment. Therefore, the greater potential carbon gain associated with a larger photosynthetic surface area must be balanced by greater water loss via transpiration and, to a lesser extent, self-shading. Thus site water balance appears to set the upper limit on the maximum leaf area a site can support. The observed relation between total leaf area and site water balance and the response of stomata within conifers to site water balance (Running 1976) suggest that environmental factors define the maximum leaf area a site can support. In support of this hypothesis, Grier and Running (1977) observed a strong positive correlation between leaf area of five Pacific Northwest forest communities and site water balance index (Figure 2).

Research reported in both the study by Grier and Running (1977) and a subsequent study by Gholz (1982) was conducted in mature stands on sites where soil fertility was not a major limitation on growth. Because of this, the reported leaf areas are probably at, or near, the maximum amount sustainable given the site water balance present at the various locations. More recent work has shown that nitrogen availability can influence the leaf biomass of individual trees and stands (Brix and Mitchell 1983, Figure 3). Specifically, leaf biomass of trees and stands occupying soils having low nitrogen availability has been shown to increase in response to nitrogen fertiliza-
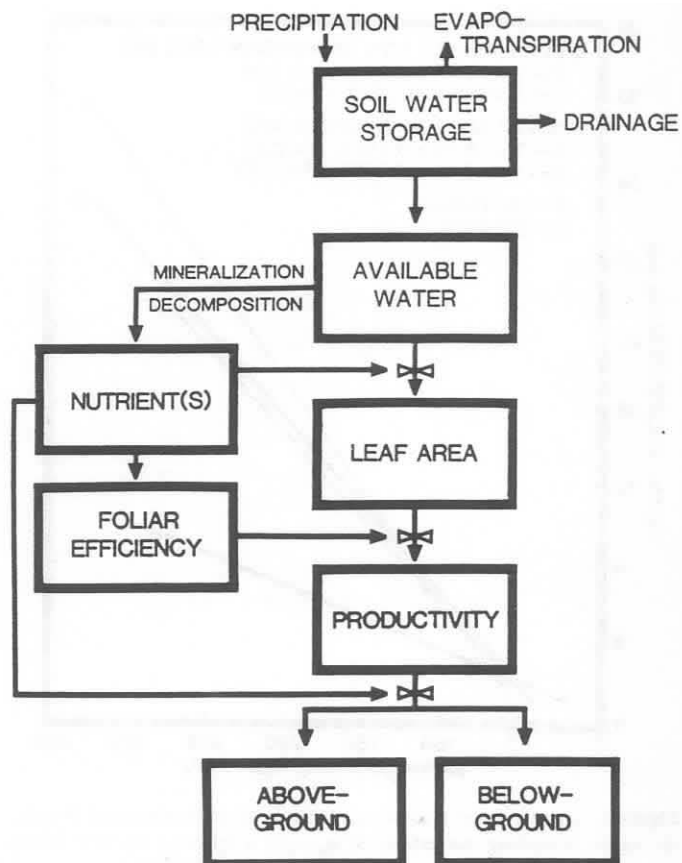
Figure 1. Conceptual model illustrating the effects of water and mineral nutrient availability on Douglas-fir productivity and carbon allocation patterns.
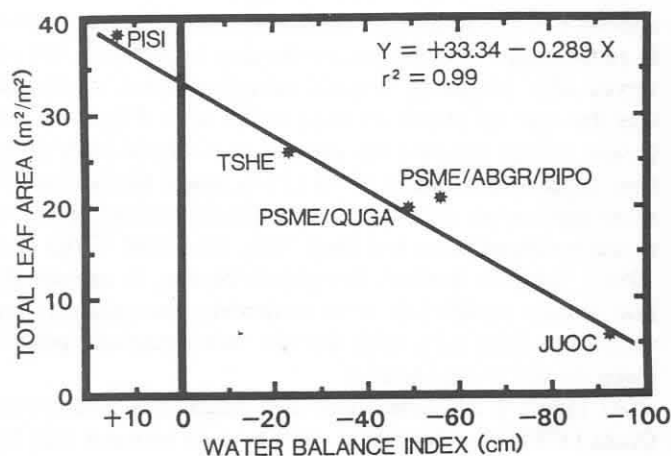
Figure 2. Relation between site water balance and total leaf area (m²/m²) for five coniferous stands in Oregon: *Picea sitchensis* (PISI), *Tsuga heterophylla* (TSHE), *Pseudotsuga menziesii/Quercus garryana* (PSME/QUGA), *Pseudotsuga menziesii/Abies grandis/Pinus ponderosa* (PSME/ABGR/PIPO), and *Juniperus occidentalis* (JUOC) (Grier and Running 1977).
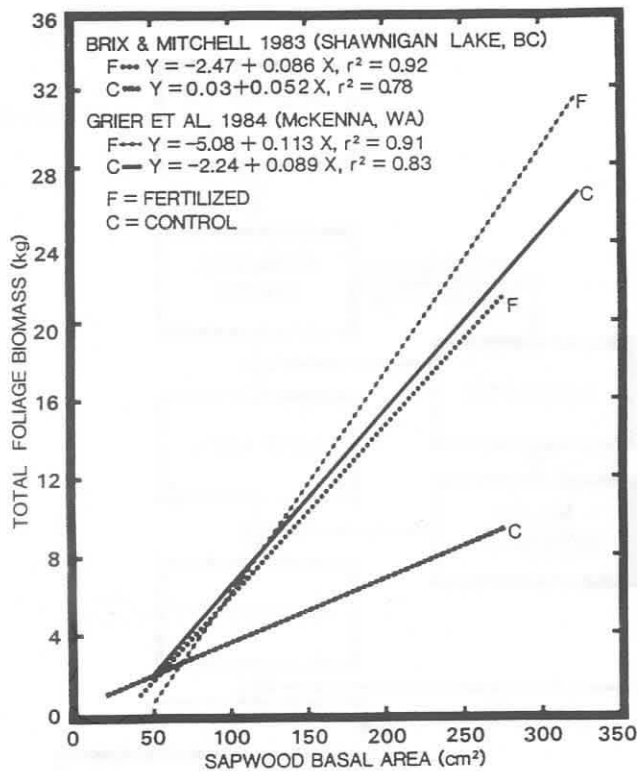
Figure 3. Comparison of regressions for fertilized and nonfertilized Douglas-fir stands illustrating the effects of nitrogen availability on total foliage biomass for low and medium site quality stands (Grier et al. 1984).

tion. This increase indicates that nitrogen limitations will prevent a stand from developing the maximum leaf areas potentially sustainable based on the site's water balance.

The response of leaf area to increased nitrogen availability appears to be related to the degree of nitrogen limitation prior to fertilization. A much greater increase in leaf area was observed after fertilizing severely nitrogen-limited stands than was the case for stands on more fertile soils (Figure 3). The greater foliage biomass and area on more fertile or fertilized sites appears to be the result of (1) increased needle size, (2) more needles per shoot, and (3) a greater number of current shoots produced (Brix and Ebell 1969, Brix 1981, Grier et al. 1984). Thus, in lowland Douglas-fir forests, it appears that low nutrient availability (most commonly nitrogen) may prevent a site from supporting the leaf area potentially possible given the site's water balance.

As Figure 1 illustrates, leaf area determines productivity. Gholz (1982) has observed a close relation between total leaf area and aboveground net primary production (Figure 4) while Schroeder et al. (1982) have shown a close agreement between stand leaf area and stemwood production in mixed conifer stands in eastern Washington. It is assumed that leaf area would also be related to total productivity.

In addition to its effect on leaf area, nutrition appears to in-

fluence stand productivity through its effect on the photosynthetic efficiency (net photosynthesis per unit of leaf area) of stand leaf area (Brix 1983). A review by Natr (1975) suggests that an inadequate supply of any essential macro- and micronutrients decreases the foliar efficiency in higher plants. Brix (1971, 1981) reported significantly greater photosynthetic rates for nitrogen-fertilized Douglas-fir trees growing on poor sites than was observed for unfertilized trees, although the response was short-lived. Similar results have been reported for coniferous species such as *Pinus pinaster* (Keay et al. 1968) and *Pinus sylvestris* (Linder and Axelsson 1982). Brix (1981) suggested that the increase in photosynthetic rate in response to nutrient amendment may be explained by one of several mechanisms: (1) increased photochemical reaction as a result of greater chlorophyll concentrations (Brix 1971, Turner and Olson 1976), (2) increased carboxylating enzyme activity (Natr 1975), (3) increased mesophyll conductance of carbon dioxide (Ryle and Hesketch 1969, Nevins and Loomis 1970, Brix 1971, Linder and Troeng 1980), or (4) increased carbon dioxide sink demand (Sweet and Wareing 1966).

At any rate, nutrition appears to influence productivity directly through its effects on stand leaf area (Figure 1) or on the photosynthetic efficiency of that leaf area. If nutrients are read-
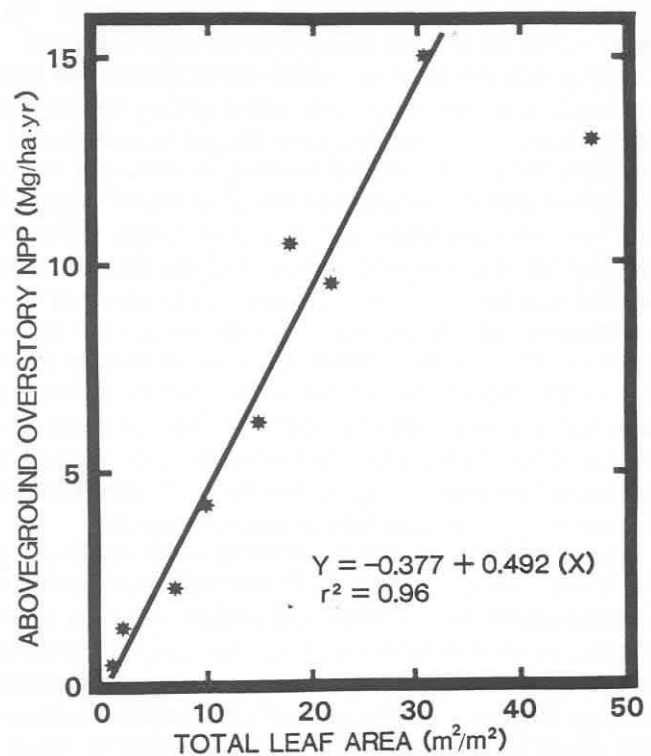

Figure 4. Relation between total leaf area (m²/m²) and aboveground overstory net primary production in nine vegetation zones of the Pacific Northwest, along a transect from the Pacific Coast to the east slopes of the Cascade Mountains (Gholz 1982).

ily available, then a site's maximum potential leaf area can be achieved; however, as nutrient availability decreases, so does the proportion of the site's potential leaf area actually achieved (Figure 3). High nutrient availability also affects the production efficiency of the existing foliage (Figure 5). If nutrients
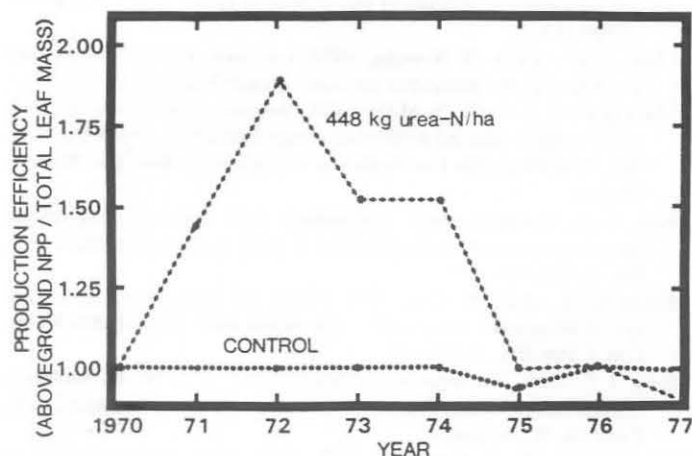
Figure 5. Effects of urea-nitrogen fertilization (448 kg N/ha) on foliar photosynthetic efficiency (aboveground dry matter production per unit of total leaf mass) (adapted from Brix 1983).

are not limiting, then a stand's productivity is set by the leaf area (Figure 4).

Mineral nutrition also influences apparent productivity of a stand through its effect on carbon allocation to above- and below-ground stand components. Keyes and Grier (1981) reported aboveground NPP for high and low productivity Douglas-fir stands to be 13.7 and 7.3 Mg/ha per year, respectively, while below-ground NPP on the productive site was 4.1 Mg/ha versus 8.1 Mg/ha per year on the poorer site (Figure 6). They
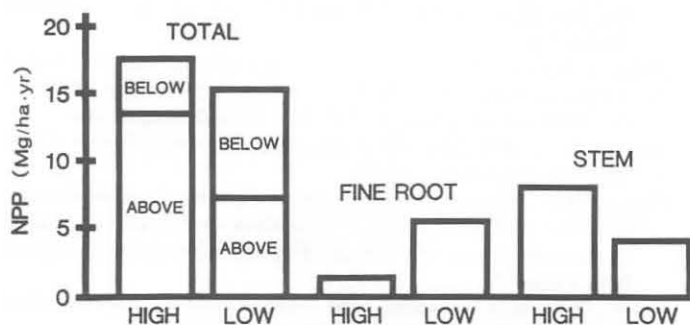

Figure 6. Above- and below-ground NPP patterns (Mg/ha·yr) for high and low site quality Douglas-fir stands (adapted from Keyes and Grier 1981).

speculated that the difference in productivity between the two sites was caused by differences in nutrient availability. In similar stands Vogt et al. (1985) observed a greater allocation of

carbon to below-ground components in control than urea-nitrogen fertilized stands of Douglas-fir (Figure 7). This paper hypothesizes that on nutrient poor sites, Douglas-fir invests a greater total amount of carbon below ground in short-lived fine roots to enhance nutrient acquisition.

When the relationship between leaf area and aboveground net primary production was analyzed for twenty-eight Doug-
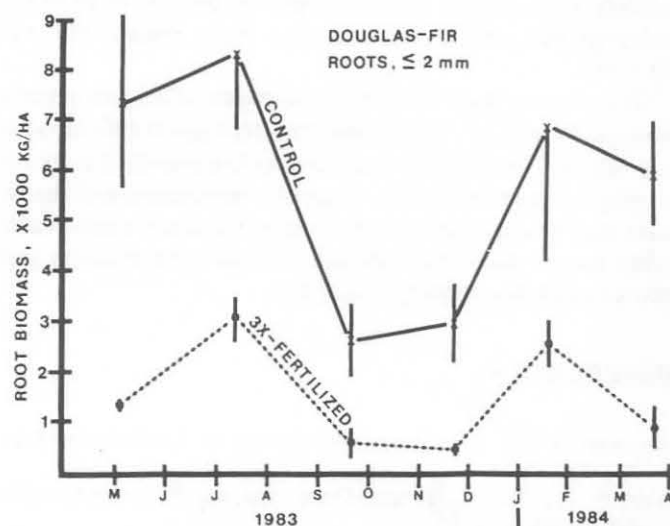
Figure 7. Long-term effects of urea-nitrogen fertilization on fine root biomass for medium site quality Douglas-fir stands in western Washington. The fertilization regime comprised three N fertilizer applications as urea (initial application rate of 448 kg/ha followed by two applications of 224 kg/ha at three-year intervals) (Vogt et al. 1985).
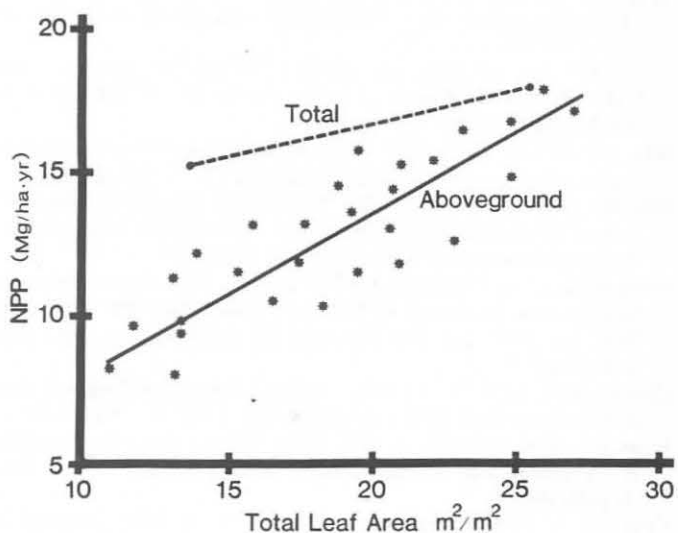
Figure 8. Total and aboveground net primary production as a function of total leaf area in selected lowland Douglas-fir stands in western Washington and Oregon. Data from Keyes and Grier (1981) and the Regional Forest Nutrition Research Project.

las-fir stands, a significant relationship was observed (Figure 8). Only two stands were available to describe the relationship between leaf area and total net primary production (Keyes and Grier 1981). Although the total NPP is sensitive to changes in leaf area, it is not as responsive to leaf area as aboveground production is. This study hypothesizes that the difference between these two lines represents below-ground production. Changes in site quality, as it affects site water balance and site nutrient status, have a dramatic impact on the ratio of above- to below-ground productivity and, to a lesser extent, total productivity.

The effect of water availability on carbon allocation patterns is currently unclear. Santantonio and Hermann (1985) reported a greater below-ground production in Douglas-fir forests occurring on more xeric sites. However, interpretation of the results may be confounded by the strong influence water availability has on decomposition and nutrient mineralization (see above) and hence nutrient availability.

REFERENCES

Alexander, M. 1977. Introduction to soil microbiology. John Wiley and Sons, New York. 467 p.

Assmann, E. 1970. The principles of forest yield study. Pergamon Press, Oxford and New York. 506 p.

Atkinson, W. A., and I. G. Morrison. 1975. The Pacific Northwest regional fertilization project, an integrated approach to forest nutrition research. *In* B. Bernier and C. H. Winget (eds.) Forest soils and forest land management, pp. 477–484. Les Presses de l'Université Laval, Quebec.

Brix, H. 1971. Effects of nitrogen fertilization on photosynthesis and respiration in Douglas-fir. For. Sci. 17(4):407–414.

———. 1981. Effects of nitrogen fertilizer source and application rates on foliar nitrogen concentration, photosynthesis, and growth of Douglas-fir. Can. J. For. Res. 11:775–780.

———. 1983. Effect of thinning and nitrogen fertilization on growth of Douglas-fir: Relative contribution of foliage quantity and efficiency. Can. J. For. Res. 13:167–175.

Brix, H., and L. F. Ebell. 1969. Effects of nitrogen fertilization on growth, leaf area and photosynthesis rate in Douglas-fir. For. Sci. 15:189–196.

Brix, H., and A. K. Mitchell. 1983. Thinning and nitrogen fertilization effects on sapwood development and relationships of foliage quantity to sapwood area in Douglas-fir. Can. J. For. Res. 13:384–389.

Curtis, R. O., G. W. Clendenen, and D. J. DeMars. 1981. A new stand simulator for coast Douglas-fir: DFSIM user's guide. USDA For. Serv. Gen. Tech. Rep. PNW–128. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon. 79 p.

Edmonds, R. L. 1979. Decomposition and nutrient release in Douglas-fir needle litter in relation to stand development. Can. J. For. Res. 9:132–140.

Fogel, R., and K. Cromack, Jr. 1977. Effect of habitat and substrate quality in Douglas-fir litter decomposition in western Oregon. Can. J. Bot. 55:1632–1640.

Gessel, S. P., E. C. Steinbrenner, and R. E. Miller. 1979. Response of Northwest forests to elements other than nitrogen. *In* S. P. Gessel, R. M. Kenady, and W. A. Atkinson (eds.) Proceedings: Forest Fertilization Conference, pp. 140–149. College of Forest Resources, University of Washington, Seattle.

Gessel, S. P., T. N. Stoate, and K. J. Turnbull. 1969. The growth behavior of Douglas-fir with nitrogenous fertilizer in western Washington. Institute of Forest Resources, College of Forest Resources, University of Washington, Seattle.

Gholz, H. L. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ecology 63:469–481.

Grier, C. C., K. M. Lee, and R. M. Archibald. 1984. Effect of urea fertilization on allometric relations in young Douglas-fir trees. Can. J. For. Res. 14:900–904.

Grier, C. C., and S. W. Running. 1977. Leaf area of mature northwestern coniferous forests: Relation to site water balance. Ecology 58:893–899.

Harrington, C. A., and R. E. Miller. 1979. Response of a 110-year-old Douglas-fir stand to urea and ammonium nitrate fertilization. USDA For. Serv. Res. Note PNW–336. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon.

Keay, J., A. G. Turton, and N. A. Campbell. 1968. Some effects of nitrogen and phosphorus fertilization of *Pinus pinaster* in Western Australia. For. Sci. 14:408–417.

Keyes, M. R., and C. C. Grier. 1981. Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Can. J. For. Res. 11:599–605.

King, J. E. 1966. Site index curves for Douglas-fir in the Pacific Northwest. Weyerhaeuser Forestry Paper 8. Weyerhaeuser Company Research Center, Centralia, Washington.

Linder, S., and B. Axelsson. 1982. Changes in carbon uptake and allocation patterns as a result of irrigation and fertilization in a young *Pinus sylvestris* stand. *In* R. H. Waring (ed.) Carbon uptake and allocation in subalpine ecosystems as a key to management. pp. 38–44. Forest Research Laboratory, Oregon State University, Corvallis.

Linder, S., and D. A. Rook. 1984. Effects of mineral nutrition on carbon dioxide exchange and partitioning of carbon in trees. *In* G. D. Bowen and E. K. S. Nambiar (eds.) Nutrition of plantation forests, pp. 211–236. Academic Press, London.

Linder, S., and E. Troeng. 1980. Photosynthesis and transpiration of 20-year-old Scots pine. *In* T. Persson (ed.) Structure and function of the northern coniferous forests: An ecosystem study. Ecol. Bull. 32 (Stockholm).

McArdle, R. E., W. H. Meyer, and D. Bruce. 1961. The yield of Douglas-fir in the Pacific Northwest. USDA Tech. Bull. 201 (rev.). 74 p.

McColl, J. G. 1969. Ion transport in a forest soil: Models and mechanisms. Ph.D. diss., University of Washington, Seattle. 214 p.

Miller, R. E., and C. A. Harrington. 1979. Response to urea and ammonium nitrate fertilization in an 80-year-old Douglas-fir stand. USDA For. Serv. Res. Note PNW–330. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon. 5 p.

Miller, R. E., and L. V. Pienaar. 1973. Seven-year response of 35-year-old Douglas-fir to nitrogen fertilizer. USDA For. Serv. Res. Pap. PNW–165. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon. 24 p.

Mooney, H. A. 1972. The carbon balance of plants. Annual Review of Ecology and Systematics 3:315–346.

Natr, L. 1975. Influence of mineral nutrition on photosynthesis and the use of assimilates. *In* J. P. Cooper (ed.) Photosynthesis and productivity in different environments, pp. 537–555. IBP Programme 3. Cambridge University Press, London.

Nevins, D. J., and R. S. Loomis. 1970. Nitrogen nutrition and photosynthesis in sugar beet (*Betula vulgaris* L.). Crop Science 10:21–25.

Running, S. W. 1976. Environmental control of leaf water conductance in conifers. Can. J. For. Res. 6:104–112.

Ryle, G. J. A., and J. D. Hesketh. 1969. Carbon dioxide uptake in nitrogen deficient plants. Crop Science 9:451–454.

Santantonio, D., and R. K. Hermann. 1985. Standing crop, production, and turnover of fine roots on dry, moderate, and wet sites of mature Douglas-fir in western Oregon. Ann. Sci. For. 42:113–142.

Schroeder, P. E., B. McCandlish, R. H. Waring, and D. A. Perry. 1982. The relationship of maximum canopy leaf area to forest growth in eastern Washington. Northwest Science 56:121–130.

Steinbrenner, E. C. 1979a. Characteristics of Northwest forest soils in relation to productivity. *In* S. P. Gessel, R. M. Kenady, and W. A. Atkinson (eds.) Proceedings: Forest Fertilization Conference, pp. 10–14. College of Forest Resources, University of Washington, Seattle.

_____. 1979b. Forest soil productivity relationships of the Douglas-fir region. *In* Forest soils of the Douglas-fir region, pp. 199–229. Cooperative Extension Services, Washington State University, Pullman.

Sweet, G. B., and P. F. Wareing. 1966. The role of plant growth in regulating photosynthesis. Nature (London) 210:77–79.

Swift, N. J., O. W. Heal, and J. M. Anderson. 1979. Decomposition in terrestrial ecosystems. Vol. 5 of Studies in Ecology. University of California Press, Berkeley. 372 p.

Turner, J. 1977. Effect of nitrogen availability on nitrogen cycling in a Douglas-fir stand. For. Sci. 23:307–316.

Turner, J., and P. R. Olson. 1976. Nitrogen relations in a Douglas-fir plantation. Annals of Botany 40:1185–1193.

Vitousek, P. M., J. R. Gosz, C. C. Grier, J. M. Melillo, and W. A. Reiners. 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecol. Monogr. 52:155–177.

Waring, R. H. 1983. Coupling stress physiology to ecosystem analysis. *In* R. H. Waring (ed.) Carbon uptake and allocation in subalpine ecosystems as a key to management, pp. 5–8. Forest Research Laboratory, Oregon State University, Corvallis.

Waring, R. H., and J. F. Franklin. 1979. Evergreen coniferous forests of the Pacific Northwest. Science 204:1380–1386.

Waring, R. H., and S. W. Running. 1978. Sapwood water storage: Its contribution to transpiration and effect upon water conductance through the stems of old growth Douglas-fir. Plant, Cell and Environment 1:131–140.

Vogt, K. A., D. J. Vogt, E. E. Moore, W. Littke, C. C. Grier, and L. Leney. 1985. Estimating Douglas-fir fine root biomass and production from living bark and starch. Can. J. For. Res. 15:177–179.